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BIODIVERSITY RESEARCH

The impact of shrub encroachment on savanna bird diversity from local to regional scale

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ABSTRACT

Aim Evidence is accumulating of a general increase in woody cover of many savanna regions of the world. Little is known about the consequences of this widespread and fundamental ecosystem structural shift on biodiversity.

Location South Africa.

Methods We assessed the potential response of bird species to shrub encroachment in a South African savanna by censusing bird species in five habitats along a gradient of increasing shrub cover, from grassland/open woodland to shrubland dominated by various shrub species. We also explored historical bird species population trends across southern Africa during the second half of the 20th century to determine if any quantifiable shifts had occurred that support an ongoing impact of shrub encroachment at the regional scale.

Results At the local scale, species richness peaked at intermediate levels of shrub cover. Bird species composition showed high turnover along the gradient, suggesting that widespread shrub encroachment is likely to lead to the loss of certain species with a concomitant decline in bird species richness at the landscape scale. Finally, savanna bird species responded to changes in vegetation structure rather than vegetation species composition: bird assemblages were very similar in shrublands dominated by *Acacia mellifera* and those dominated by *Tarchonanthus camphoratus*.

Main conclusions Shrub encroachment might have a bigger impact on bird diversity in grassland than in open woodland, regardless of the shrub species. Species recorded in our study area were associated with historical population changes at the scale of southern Africa suggesting that shrub encroachment could be one of the main drivers of bird population dynamics in southern African savannas. If current trends continue, the persistence of several southern African bird species associated with open savanna might be jeopardized regionally.

Keywords

Biome shift, bush encroachment, global change, land cover change, landscape heterogeneity.

INTRODUCTION

Ecosystem dynamics are increasingly forced by global change factors including land-use changes, rising atmospheric CO_2 concentration, nitrogen deposition, acid rain, changes in fire regimes, climatic shifts, or biotic exchanges (Sala *et al.*, 2000; Steffen *et al.*, 2004). Studies on the ecological impacts of global changes have often focused on individual drivers (e.g. temperature increase, deforestation), mainly in northern temperate ecosystems. However, many of these global change drivers interact in complex ways and affect both northern and southern hemispheres. For instance, the importance of atmospheric CO_2 level in contributing to the dramatic increase in woody plant cover observed across the world during the last 50–100 years may have been underestimated (Bond & Midgley, 2000), but a lack of key information limits the clear distinction of CO_2 level from a complex of other interacting drivers (e.g. Scholes & Archer, 1997). This woody

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cover increase, often referred as shrub encroachment, has been documented in arctic (Sturm *et al.*, 2001), subalpine (Anthelme *et al.*, 2007), Mediterranean (Mazzoleni *et al.*, 2004), savanna (Roques *et al.*, 2001) and desert biomes (Goslee *et al.*, 2003). As landscape changes associated with woody cover increase occur at relatively slow rates similar to natural succession, shrub encroachment is often perceived as a 'natural' process, yet this change represents a biome switch with potentially substantive biodiversity impacts (Fischlin *et al.*, 2007).

Savannas are defined by the coexistence of trees and grasses (Scholes & Archer, 1997), and occupy a fifth of the earth's land surface (Sankaran *et al.*, 2005). Despite widespread and sometimes locally intense tree removal for firewood (Anderson & Anderson, 2001), shrub encroachment of savannas has occurred under a range of climatic, soil or management conditions in North (Archer, 1989) and South America (Adamoli *et al.*, 1990), Australia (Burrows *et al.*, 1990), India (Singh & Joshi, 1979) and Africa (Vanvegten, 1984). Savannas are important as rangelands, and the consequences of shrub encroachment for livestock productivity were assessed as early as the beginning of the 20th century (West, 1947). More recently, shrub encroachment has been acknowledged as the first step of a biome shift potentially threatening savannas (Scheffer *et al.*, 2001). In mesic savannas, the shift from open grassland to acacia savanna woodland to closed canopy broadleaf thickets can occur within 40 years (Skowno *et al.*, 1999). This rapid and widespread woody cover increase results in a decrease of open savannas (Roques *et al.*, 2001) and vegetation homogenization at landscape and regional scales (Sheuyange *et al.*, 2005).

These dramatic changes in savanna shrub cover have been shown to affect the species diversity of dung beetles (Steenkamp & Chown, 1996), lizards (Meik *et al.*, 2002), rodents (Blaum *et al.*, 2006), mammalian carnivores (Blaum *et al.*, 2007) and arthropods (Blaum *et al.*, 2009). Bird species have been shown to differ between contrasting habitats (grassland versus woodland; Skowno & Bond, 2003), contrasting land uses (protected versus non-protected; Herremans, 1998) and contrasting management (encroached versus tree removal; Kaphengst & Ward, 2008). However, the variations of bird assemblages along a gradient of woody cover increase have received surprisingly little attention in a system characterized by its heterogeneity (Tews *et al.*, 2004).

How might shrub encroachment affect bird species richness? The 'habitat heterogeneity hypothesis' assumes that structurally complex habitats may provide more niches and diverse ways of exploiting environmental resources, thus increasing species diversity (Bazzaz, 1975). Thus, shrub encroachment is expected to result in an increase of bird species richness. Similar increases in species richness due to shrub encroachment have already been documented in other biomes (Rosenstock & Van Riper, 2001). Is this pattern observed both at the local scale (plot = 3 ha) and the landscape scale (study site = 10,000 ha)? Secondly, does shrub encroachment influence bird species composition? If yes, then is species turnover constant along the gradient of shrub encroachment? Thirdly, what is the relative importance of vegetation structure (physiognomy) and vegetation composition (floristics)? Although vegetation structure is acknowledged as the most important factor influencing the general distribution of birds (MacArthur & MacArthur, 1961), several studies showed that floristics can have the greatest potential to influence community composition at a local scale (Rotenberry, 1985; Fleishman *et al.*, 2003). Similarly, does encroachment by different shrub species have similar impacts on bird assemblages? Encroachment of shrub species with distinct morphological and chemical characteristics would be expected to have distinct impacts on bird assemblages (Greenberg *et al.*, 1997). Finally, what is the relationship between long-term trends of bird population in southern Africa and shrub encroachment? Shrub encroachment has occurred in many parts of southern Africa over recent decades. If it is the main driver of species population dynamics in savanna, then species associated with open savanna would be expected to show population declines, while those associated with closed savanna would be expected to show increases.

To address these questions, we studied bird assemblages along a vegetation structure gradient, using space-for-time substitution in order to assess the impact of shrub encroachment on bird communities. We selected a study area in a southern African savanna that has experienced shrub encroachment during the last 50 years.

METHODS

Study site

The study area was located in the Rooiport Nature Reserve, 60 km west of Kimberley in South Africa' Northern Cape province (28°35′ S; 24°14′ E). The study area was selected in order to include patches of different vegetation structures, ranging from grassland to woodland with different level of shrub encroachment. It covers 10,000 ha of a plain on deep red-brown and yellow-brown sands with an average altitude of 1100 m. The rainfall is erratic and occurs mainly during summer (January–March) with an average of 425 ± 132 mm year^{-1} and the temperature extremes are from minimum temperatures of −4 °C during the coldest months to maxima of 44 °C in the summer (Land Type Survey Staff 1986). The study area has been managed as a game hunting reserve since 1893, except between 1930 and 1947 when it was used for domestic stock farming. After the 1950s, it was managed as a private nature reserve. Vegetation at the site is Kimberley Thornveld and Vaalbos Rocky Shrubland (Mucina & Rutherford 2006), and comprise open savanna with mature *Acacia erioloba* and *Acacia tortilis* interspersed in a grassy layer dominated by *Eragrostis lehmanniana* and a number of *Aristida* spp. In areas in which bush thickening has occurred, the shrub species *Acacia mellifera, Rhigozum trichotomum, Grewia flava* and *Tarchonanthus camphoratus* have become the dominant species.

Vegetation categories

We defined five structural categories of vegetation (modified from Pratt *et al.* (1966): grassland (G = grasses plus other annual herbs, short shrubs covering < 10%); shrubby grassland (SG = grasses plus other annual herbs, short shrubs covering between 10 and 25%, shrubs ranging from 0.5 to 3 m in height); shrubland (S = shrubs ranging from 0.5 to 3 m in height covering more than 25% with trees smaller than 5 m); open woodland (OW = grasses plus other annual herbs, trees > 5 m representing < 25%) and shrubby woodland (SW = mix of grasses, shrubs and trees > 5 m, with woody cover representing between 25 and 50%). We used aerial photographs from the year 2001 combined with ground-truthing in order to locate patches with different vegetation structure. We selected 10 census-plots randomly in each of the five categories. Plots were located at least 200 m away from rivers or rocky areas and at least 500 m apart from each other in order to minimize spatial autocorrelation.

In order to assess the impact of the increase in woody cover owing to different shrub species, we compared two shrub species: *Tarchonanthus camphoratus* (t) and *Acacia mellifera* (a) and two structural categories: shrubby grassland and shrubland. Plots of these two structural categories were split equally in patches dominated by the two shrub species. We selected 20 supplementary plots (five in each structural category for each shrub species). As a result we assessed the impact of the increase in woody cover owing to different shrub species by analyzing differences in bird assemblages using 40 plots (10 plots in each structural category for each shrub species: SGt, SGa, St and Sa).

Bird community sampling

Bird communities were surveyed at the 70 census-plots during a single visit by C. Sirami in January 2008. Birds seen or heard within a radius of 100 m were counted during a 10-min point count. This plot size (equivalent to 3 ha) corresponds to the maximum distance within which most of the species are usually detected (Sirami *et al.*, 2007) and minimizes double counting as plots were at least 500 m apart from each other. Censuses were restricted to clear, windless days within 4 h after sunrise (the period of peak vocal activity). Raptors, aerial feeders (swallows, swifts and bee-eaters) and crepuscular species were excluded from the analysis because the point-count method is inappropriate for assessing their abundance (Bibby *et al.*, 1992).

Vegetation structure and composition

The vegetation structure was assessed within a 25-m radius of the survey point, visibility being impaired beyond this distance in closed habitat. For each census-plot, we estimated cover of tree (> 3 m), shrub (< 3 m), tall grass (> 0.2 m), short grass (< 0.2 m), forb, bare ground as well as the maximal height of the vegetation canopy (h_{max}) and the height at which the vegetation canopy had a cover exceeding 25% (h_{main}). Vegetation composition was assessed by recording the two dominant tree species, the two dominant shrub species and the two dominant grass species.

Analyses

Vegetation structure

We calculated the average value for the eight variables describing the vegetation structure for each one of the five structural categories as well as for the four structural categories with different shrub species. In order to test for a relationship between vegetation structural diversity and shrub cover, we computed Shannon Diversity Index for each census-plot [$I = -\Sigma p_i$ ($\log p_i$) with p the cover percentage and i the six variables of vegetation cover]. We tested for relationship between vegetation structural diversity and shrub cover using linear models [generalized linear model (GLM) with normal distribution] in the program R (R Development Core Team 2008). Vegetation structural diversity (veg div) was the dependent variable; shrub cover and shrub cover^2 were the independent variables. Independent factors were added sequentially to the model, and the final model was selected based on the minimum Akaike information criterion (AIC) (Burnham & Anderson, 2002). Spatial autocorrelation of a response variable can lead to bias in fitted models (Lennon *et al.*, 2001). We tested for autocorrelation in the vegetation structural diversity using Moran's *I*-test implemented in the package 'SPDEP' (Bivand & Contributors, 2009) in R. The result of this test (Moran *I*-statistic standard deviate = 0.9316, *P*-value = 0.1746) suggested no apparent spatial autocorrelation in the vegetation structural diversity.

Bird species richness

At the local scale (census-plot), we tested for relationships of bird species richness with shrub cover following the procedure described for vegetation diversity. We used GLMs with species richness (number of species detected within a plot) as the dependent variable; shrub cover, shrub cover^2 and veg div as the independent variables. We assumed a Poisson distribution for the dependent variable and a logarithmic link function. Independent factors were added sequentially to the model, and the final model was selected based on the minimum AIC. We tested for spatial autocorrelation in species richness data. The result of the Moran's *I*-test suggested no apparent spatial autocorrelation in species richness (Moran *I*-statistic standard deviate = −0.2206, *P*-value = 0.5873).

At the landscape scale (study area), we estimated bird species richness in each structural category (five categories) using the software EstimateS (Colwell, 2006), which takes into account differences in species detection probabilities. We computed five species richness estimators that have been shown to be reliable in previous studies: the incidence-based estimators ICE and Chao 2, first and second-order Jackknife estimators, and the Bootstrap estimator (see Colwell & Coddington, 1994; Hortal *et al.*, 2006). We calculated the mean of the five estimators for each structural category and compared the means between the five categories using paired *t*-tests with a correction for unequal variances in the program R (R Development Core Team 2008).

Bird species composition

We used analysis of similarity (ANOSIM; Carr, 1996) to test for differences in bird assemblages across the five structural categories. The ANOSIM procedure uses Monte Carlo randomization of observed data to assess whether rank similarities within groups are greater than between groups. The Sorensen distance was used to express similarities, and 1000 Monte Carlo permutations were conducted to generate a random test statistic (Carr, 1996). This analysis was conducted first for all five structural categories together, and then for pairwise *post hoc* comparisons. We compared the mean distance between categories using paired *t*-tests in the program R (R Development Core Team 2008).

The respective roles of vegetation composition and vegetation structure for bird species composition were assessed using similarity matrices and Mantel tests following Fleishman *et al.* (2003). We calculated the Canberra distance between all pairs of census-plots for species composition of bird (57 species), vegetation structure (eight variables) and vegetation composition (20 species). We also calculated Euclidean distances between all pairs of census-plots. First, we used Mantel (Mantel, 1967) tests to test whether similarity of bird assemblages was a function of distance between census-plots. Then we evaluated whether vegetation structure and vegetation composition were correlated. We used Partial Mantel tests to test whether species composition of birds was correlated with vegetation composition after controlling for vegetation structure, and correlated with vegetation structure after controlling for vegetation composition.

Encroachment by different shrub species

The relative impacts of encroachment by different shrub species were analysed by comparing the two types of shrubby grassland and the two types of shrubland. We estimated bird species richness in each vegetation type (four categories) following the procedure described previously using EstimateS (Colwell, 2006). We used ANOSIM to test for differences in bird assemblages across the four vegetation types.

Population long-term trends

Our last objective was to assess the relationship between species position along the gradient of woody cover increase and temporal changes in species population in southern Africa. First we performed a canonical correspondence analysis (CCA), a multivariate method that relates community composition to environmental variables, assuming a unimodal response of species occurrence. As the different variables of vegetation structure were correlated, we performed a principal component analysis (PCA) on the eight variables, and used the scores along the first four components of the PCA. We performed CCA on the 57 species × samples matrix with the four PCA components as environmental variables. We plotted species according to their score along the two first axes of the CCA. Species were considered decreasing or increasing according to the available literature synthesized in Hockey *et al.* (2005). Species were considered as showing a trend towards population decrease when regional decrease in population, regional extinction or range contraction was documented. Species were considered as showing a trend towards population increase when regional increase in population or range expansion was documented. The other species were considered as showing no trend.

RESULTS

Vegetation structure

The average vegetation structure of the five vegetation categories and four vegetation types is presented in Table 1. Vegetation structural diversity was best explained (lowest AIC) by the model that included shrub and shrub^2 (Table 2). Vegetation structural diversity peaked at intermediate shrub cover (Fig. 1).

Bird species richness

Local bird species richness (lowest AIC) was best explained by the model that included shrub and shrub^2 (Table 2). Local bird

Table 1 Average vegetation structure of the five structural vegetation categories and the four vegetation types (values are cover percentage except $h_{\max}$ and h_{main} in metres).

	Tree	Shrub	Tall grass	Short grass	Forb	Bareground	$h_{\max}$	h_{main}
Grassland	0.5	1.2	45.3	16.0	13.4	25.4	3.3	0.6
Shrubby grassland	0.3	16.5	46.6	2.3	22.4	28.6	3.3	0.6
Shrubland	0.6	50.0	26.0	0.7	11.5	61.8	4.2	1.8
Open woodland	11.0	8.5	52.3	3.9	10.5	33.3	7.0	1.3
Shrubby woodland	20	31.5	39.0	0.6	17.3	43.1	7.3	3.7
SG *Acacia*	0.2	22.0	43.3	2.1	14.2	40.5	3.1	1.1
SG *Tarchonanthus*	0.8	20.0	36.4	4.6	24.2	34.8	4.1	0.8
S *Acacia*	0.4	56.0	25.5	0.6	11.0	62.9	3.9	2.1
S *Tarchonanthus*	0.7	44.0	17.2	3.2	14.3	65.4	4.1	1.7

Table 2 Generalized linear models for the relationship of vegetation structural diversity and bird species richness (SR) with shrub cover (shrub cover and shrub cover^2) and vegetation diversity (veg div): coefficient ± standard error (SE), z-statistic (z; $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$), degree of freedom (d.f.), Akaike Information Criterion (AIC).

	Coefficient (±SE)	z	Residual deviance	d.f.	AIC
Vegetation diversity					
Intercept	4.99e-01 (±2.63e-02)	18.95***	0.584	49	−76.53
Shrub cover	7.95e-03 (±2.29e-03)	3.47**	0.576	48	−75.27
Shrub cover^2	−1.39e-04 (±3.5e-05)	−3.95***	0.432	47	−87.59
Bird SR					
Intercept	2.0632 (±0.0936)	22.04***	37.13	49	244.94
Shrub cover	0.0200 (±0.0076)	2.621**	31.93	48	241.74
Shrub cover^2	−0.0002 (±0.0001)	−2.04*	27.67	47	239.48
Veg div	0.3208 (±0.5004)	0.641	27.26	46	241.06

species richness peaked at intermediate shrub cover (Fig. 2). At the landscape scale, species richness varied significantly with structural category. Species richness was significantly higher in shrubland than in shrubby grassland, open woodland and shrubby woodland, and significantly higher in shrubby grassland than in open woodland (Fig. 3).

Bird species composition

Similarities in bird species composition were greater within structural categories than between these same categories (ANOSIM, global $R = 0.4901$, P-value < 0.001, Table 3). Every structural category had a distinctive bird species composition (pairwise tests, $P < 0.01$ in all cases except between shrubby grassland and shrubland $R = 0.0473$, P-value = 0.246). The similarity in bird species composition between grassland and shrubby grassland was lower (52.51) than for other transitions (SG–S, OW–SW and SW–S) although the difference was not significant.

There was no correlation between bird species composition and distance between census-plots (Table 4). Vegetation composition and structure were strongly correlated. The correlation between bird species composition and vegetation structure after controlling for vegetation composition was significant, whereas correlation between bird species composition and vegetation composition after controlling for vegetation structure was not (Table 4).

Encroachment by distinct shrub species

Comparison of estimated species richness did not show any significant difference between shrubby grassland or shrubland dominated by *Acacia mellifera* versus *Tarchonanthus camphoratus*. Similarities in bird species composition between structural categories dominated by different shrub species were not significantly greater than similarities within these same categories (ANOSIM, global $R = -0.01772$, P-value = 0.661).

Long-term bird population trends

Among the 57 bird species recorded in this study, nine exhibited increasing populations, and five species had declining populations (see Appendix S1; Hockey *et al.*, 2005). The PCA of the vegetation structure generated four independent components: the first component (Tree) was correlated positively with tree cover, maximum canopy and average

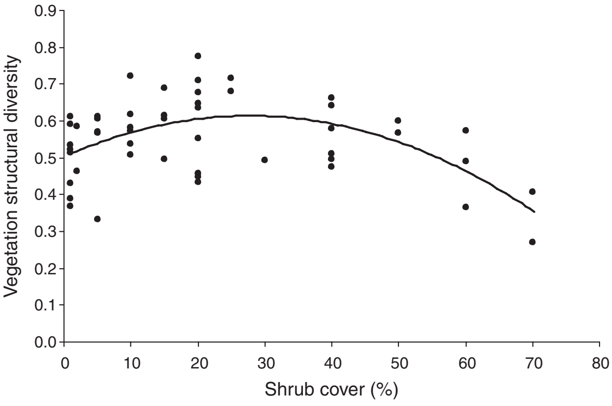

Figure 1 Vegetation structural diversity along the gradient of shrub encroachment. Symbols show observed vegetation structural diversity in the 50 plots (Shannon diversity index) plotted against the shrub cover (%). Line shows modelled vegetation structural diversity using equation in Table 2.

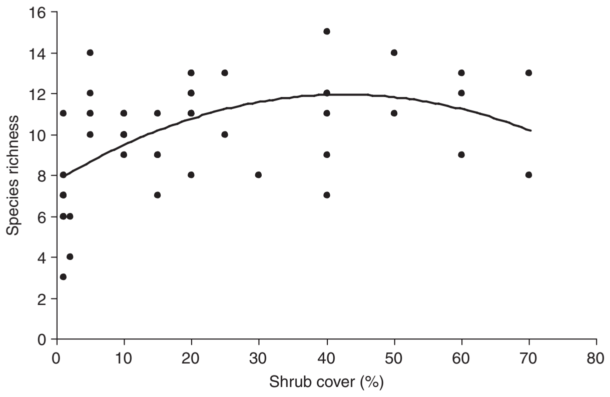

Figure 2 Species richness along the gradient of shrub encroachment. Symbols show observed species richness in the 50 plots plotted against the shrub cover (%). Line shows modelled species richness using equation in Table 2.

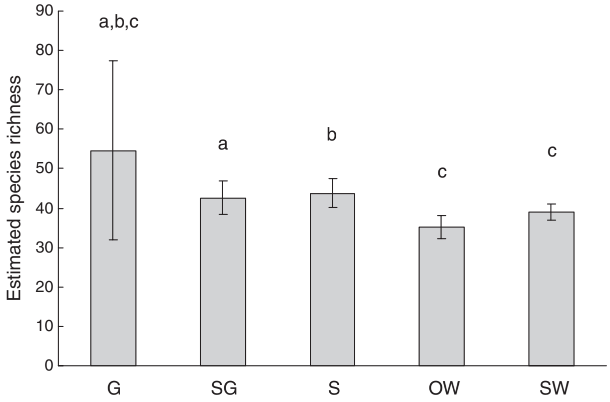

Figure 3 Estimated species richness per vegetation categories: G, grassland; SG, shrubby grassland; S, shrubland; OW, open woodland; SW, shrubby woodland. Values correspond to the mean of the five estimators used in EstimateS. Bars correspond to the standard errors. The species richness of categories without any letter in common is significantly different.

Table 3 Percentage of similarity based on bird presence–absence data between vegetation categories and within vegetation categories (values marked with *).

	G	SG	S	OW	SW
Grassland (G)	62.34*				
Shrubby grassland (SG)	52.51	61.76*			
Shrubland (S)	47.65	59.91	59.27*		
Open woodland (OW)	55.06	59.72	58.17	67.05*	
Shrubby woodland (SW)	49.02	57.27	57.41	62.55	62.14*

canopy (cf. description in methods); the second component (Shrub) was correlated positively with shrub cover; the third component (Grass) was correlated positively with tall grass cover and negatively with short grass cover and bare ground cover; and the fourth component (Forb) was correlated with forb cover. The two first axis of the CCA explained 70% of variance in bird species composition. Eight of the nine increasing species were associated with high tree and shrub cover (right part of the axis 1 and axis 2 plane of the CCA, Fig. 4). Four of the five decreasing species were associated with high grass cover (located on the left part of the axis 1 and axis 2 plane of the CCA, Fig. 4).

DISCUSSION

Temporary increase in habitat and avifauna diversity

Our results suggest that shrub encroachment generates a temporary increase in local bird species richness. Bird species richness increased significantly with shrub cover in the first part of the gradient then decreased significantly beyond 40% of shrub cover (Fig. 2). This result is consistent with the 'habitat heterogeneity hypothesis' (MacArthur & MacArthur, 1961), which predicts that structurally complex habitats provide more niches and environmental resources, and thus increase species diversity. In this study, we found that the maximum habitat diversity is reached on average around 30% of shrub cover in this area. Although the variable describing vegetation structural diversity was not selected in our final model, our results suggest that the maximum bird species richness was reached at the upper end of this heterogeneity peak around 40–50% of shrub cover. Similar responses have already been found in arthropods in other parts of the southern Kalahari (Blaum *et al.*, 2009). In these drier parts of the Kalahari (150–250 mm annual rainfall), vegetation heterogeneity peaks between 15 and 20%, with a corresponding peak of arthropod species richness. Other taxonomic groups seem to show similar hump-shaped trends of diversity in relation to shrub cover in the savanna of the southern Kalahari: rodents (Blaum *et al.*, 2006), carnivores (Blaum *et al.*, 2007) and reptiles (Wasiolka 2003).

Table 4 Correlations (Mantel's r-statistics and P-value) between species composition of birds, species composition of vegetation, vegetation structure and distance between census-plots.

Dependent var.	Independent var.	Covariate	r	P-value
Bird	Distance		−0.1022	0.966
Composition	Structure		0.3467	< 0.001
Bird	Structure	Composition	0.1127	0.022
Bird	Composition	Structure	−0.00474	0.507

We observed similar patterns when comparing the species richness per structural category, with bird species richness in shrubland significantly higher than in shrubby grassland, open woodland and shrubby woodland. However, grasslands showed a high species richness associated with a high variance. This high variance in estimated species richness is likely owing to the usually low detection probability of grassland species

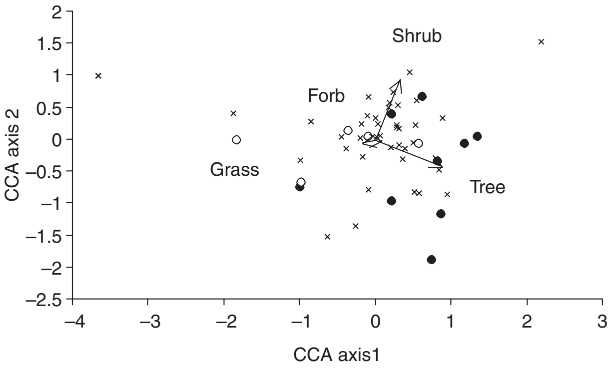

Figure 4 Axis 1 and axis 2 plane of the canonical correspondence analysis (CCA) showing the species and the four environmental variables (four factors of the Principal Component Analysis using the eight variables of vegetation structure). Symbols refer to the categorized long-term population trend of the species in southern Africa from Hockey *et al.* (2005): ○ = decreasing trend, x = no trend, ● = increasing trend.

(Diefenbach *et al.*, 2003) likely due to higher predation rates in open landscapes (Boulinier *et al.*, 1998). Despite this high variance, the high species richness can be related to both the presence of grassland specialists and the diversity of grassland types (tall versus short grassland). Krook *et al.* (2007) showed that different grassland types (e.g. grazing lawns and tall grasslands) are associated with very distinct bird assemblages. Our results suggest that while shrub encroachment has a positive impact up to a certain point on species richness at the habitat level in open woodland, it might have a more ambiguous effect in grassland.

Biotic homogenization at larger scales

Bird assemblages found in open savanna were significantly distinct from those in closed savanna, with < 50% of species in common. Seed-eaters and other birds associated with grasses decreased as the percentage of shrubs increased (e.g. Temminck's courser), whereas insectivorous species increased (e.g. Kalahari scrub-robin). A similar difference has also been observed between bird assemblages associated with grassland and acacia woodlands in Hluhluwe-Umfolozi (Skowno & Bond, 2003). At the landscape scale (study site), shrub encroachment usually results in a decrease of landscape heterogeneity due to the colonization of patches of open savanna by shrubs and the expansion of existing patches of shrubland. The relationship between shrub encroachment and landscape homogenization has been shown in other biomes (Roura-Pascual *et al.*, 2005). Shrub encroachment is likely to lead to the loss of bird species associated with open savanna in favour of those associated with closed savanna. Our study suggests that shrub encroachment is likely to result in a decrease of bird species richness at the broader landscape scale.

At the regional scale (southern Africa), our study suggests that bird species believed to be decreasing regionally were associated with open savanna, whereas those believed to be increasing were associated with closed savanna. Although the aim of the present study was not to determine the causes of these trends, our results suggest that shrub encroachment may be a significant driver of bird population dynamics in southern Africa savannas. Bird population trends in the second half of the twentieth century could have resulted from a combination of drivers, including climate change or land-use change in other biomes. Whatever the drivers of bird populations have been in the past, the current rate of shrub encroachment is likely to accelerate the past population dynamics of savanna bird species. Moreover, we suggest that if the same trends continue in future, persistence of open savanna species might be imperilled. Over the past 50 years, evidence has accumulated suggesting that woody cover increase is occurring throughout southern African savannas: Zimbabwe (West, 1947), Swaziland (Roques *et al.*, 2001), Kalahari (Jeltsch *et al.*, 1997) and Botswana (Vanvegten, 1984). Impacts of these vegetation changes on bird communities have already been observed in Ivory Coast (Thiollay, 2006) and Tanzania (Gottschalk *et al.*, 2007). As a result, species in both southern Africa and other parts of Africa might be at risk of reduced habitat availability.

Bird response to changes in vegetation structure

Bird communities seemed to be primarily controlled by vegetation structure, rather than vegetation composition. This result was confirmed by the comparison of shrub encroachment owing to different shrub species. Although *Tarchonanthus camphoratus* and *Acacia mellifera* differ strikingly in terms of morphology and secondary compound, bird communities associated with shrubland dominated by one or the other did not differ appreciably. This result suggests that vegetation structure is probably the most important feature influencing bird species assemblages and diversity in arid savannas. However, this might not be true in mesic savannas where plant species diversity is much higher, or in the case of encroachment by alien shrub species. For example, the invasion of *Prosopis glandulosa* is likely to have a rather different impact on bird communities, as stands dominated by this species have a completely different vertical structure (Dean *et al.*, 2002).

Changes in vegetation structure have similar impacts on bird species composition all along the gradient, with a minimum turnover of 37% from open woodland to shrubby woodland. There was no significant variation in species turnover among the different ecological transitions between vegetation types. However, the impact of shrub encroachment tended to be higher during the transition from grassland to shrubby grassland (only 52% of species in common) than during that from shrubby grassland to shrubland (no significant difference in bird species composition). Grassland represents a structurally homogeneous habitat in which bird grassland specialists are sensitive to a decrease in patch size (Krook *et al.*, 2007) as well as small increase in shrub cover, likely to result in a dramatic change in competition or predation (Johnson & Temple, 1990). As a result, a small increase of shrub cover is likely to result in a higher turnover in grassland than in shrubby grassland, where bird communities are already adapted to a heterogeneous habitat.

Implications for management

Considering the rate (Skowno *et al.*, 1999) and the extent (Trollope *et al.*, 1989) of shrub encroachment in southern African savannas, the conservation of savanna biodiversity poses a challenge. Shrub encroachment is likely to have the most dramatic impacts in grassland patches embedded in the savanna matrix, regardless of the shrub species. Thus, policies such as woody plant removal should prioritize the enlargement of existing grassland patches. Krook *et al.* (2007) suggest that grassland patches should have a minimum size of 8 ha in order to be suitable for specialist grassland bird species. However, woody plant removal should be very carefully implemented. Over vast areas of the Kalahari, injudicious application of arboricides targeting shrubs has led to the death of not only the target (shallow-rooted) shrub species, but all species (including deep-rooted *Acacia erioloba* and *Boscia albitrunca*). Moreover, areas treated with arboricides seem to be associated with low bird diversities, even of grassland type birds (C. Seymour, unpublished results). This low diversity could be a consequence of habitat degradation due to the chemical accumulation in the environment (Seymour, 2006). It may also result from the isolation of the cleared patches from other sources of grassland birds. Indeed, colonization of these new grassland patches is likely to be limited by species dispersal (Brotons *et al.*, 2005). Connectivity between grassland patches should thus be taken into account in management policies, for example through the maintenance of corridors of open savanna. Management of shrub encroachment is also an economic challenge in production landscapes (e.g. on cattle farms, communal lands) where it represents a reduction in carrying capacity. Although Kraaij & Ward (2006) recommended that farmers should not graze cattle heavily in years of good rainfall, Jeltsch *et al.* (1997) found that even recommended stocking rates may eventually lead to shrub encroachment within 100 years in the Kalahari. As a high proportion of the human population relies on pastoralism in southern and central Africa (Scholes & Archer, 1997), shrub encroachment might represent a threat for the livelihood of a large and rapidly growing proportion of the world's human population. This potential convergence between economic stakes and environmental stakes will help the implementation of conservation policies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of bird species recorded during the survey in Rooiport Game Reserve, South Africa, in January 2008.

BIOSKETCHES

All of the authors are interested in the effects of global change biota in southern Africa, particularly birds.

This paper results from an ongoing collaboration from a MACIS funded project investigating the impact of climate change on bird communities in southern African savannas.

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